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RESEARCH ARTICLE

The distribution and conservation status of *Tapirus terrestris* in the South American Atlantic Forest

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Abstract

Tapirus terrestris is the largest South American land mammal, with an extensive historical distribution and capable of occupying diverse habitats, and yet its populations have declined across its range. In order to provide baseline data on the conservation status of tapirs in the Atlantic Forest, we conducted a long-term study in one landscape, visited 93 forests, and received 217 expert reports over the 15-year study. We estimate that 2,665–15,992 tapirs remain in 48 confirmed populations, occupying 26,654 km^2 of forest or 1.78% of its original range in the biome. Historically, hunting and deforestation were the main causes of decline, but today population isolation is the principal long-term threat. Vortex models indicate that 31.3–68.8% and 70.8–93.8% of the populations are demographically and genetically non-viable over the next 100 years, respectively, and that only 3–14 populations are viable when considering both variables. Habitat use data indicate that tapirs are adaptable to disturbed and secondary forests and will use diverse tree plantations and agricultural lands but hunting and highways keep populations isolated. Reserve staff report tapirs as common/abundant at 62.2% of the sites, and populations as stable and growing in 60% and 36% of the sites, respectively, and there is ample habitat in the biome for a population expansion, but overcoming the causes of isolation will be necessary for this to occur. Lack of adequate funding for protecting reserves is a chronic threat throughout the biome, especially in federal and state/provincial reserves, and increased funding will be necessary to implement effective conservation plans.

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Keywords
Conservation status, hunting, isolation, lowland tapir, population viability, roads

Introduction

The lowland tapir (*Tapirus terrestris* (Linnaeus, 1758)) is the largest land mammal native to South America, weighing up to 250 kg, and can adapt to almost any habitat on the continent including wetlands, savannas, dry forest, rainforest, mangroves and alpine peaks (Padilla and Dowler 1994). Tapirs are capable of moving across any terrain from swamps to steep mountain slopes, and are excellent swimmers, taking refuge in water when pursued by predators (Padilla and Dowler 1994). It has a catholic diet that includes >200 plant species from which it eats fruits, leaves, twigs, and bark, eats mineral enriched soils and has hind-gut fermentation that allows for an efficient processing of low-quality foods (Tobler et al. 2010; Hibert et al. 2011). Amply adaptable, the species once ranged throughout the tropics and sub-tropics of South America east of the Andes Range (Padilla and Dowler 1994; García et al. 2012).

Tapirs have low reproductive potential with a single offspring produced after a gestation of 13 months and inter-birth intervals of up to 3 years (Pukazhenthi et al. 2013). Because of this, they are susceptible to rapid population declines when subject to heavy predation pressure (Bodmer et al. 1997). With conspicuous tracks, trails and feces, tapirs are easy to track, and their habit of fleeing into water as a means of escaping predators is ineffective against humans. Road-kill is also a significant cause of tapir mortality, especially in heavily fragmented biomes (Medici and Desbiez 2012). Due to hunting pressure and road-kill, this otherwise adaptable animal has disappeared from suitable habitat throughout large parts of its range (Medici et al. 2012).

At the beginning of the 16th century when Europeans arrived in the New World, tapirs were distributed throughout the 4,000 km length of the 1.5 million km^2 Atlantic Forest (Soares de Sousa 1971; Dean 1995). Over the past 500 years the decline of tapirs accompanied that of the Atlantic Forest, with the species extirpated from the populated coastal areas by the 17th century (Dean 1995) and anywhere that hunters had easy access thereafter. By the late 19th century, tapirs were extirpated from the lower slopes of the Serra do Mar from Rio de Janeiro south and in parts of the northeast, but persisted in reduced populations in the mountains and lowland areas with low human population densities. Hunters extirpated most remnant populations between the 1950s and 1970s, with few individuals tenuously surviving on the most inaccessible peaks and forests. By 1996, when we began studying tapirs in the biome, the location and conservation status of most populations was unknown. In light of an apparent widespread decline, it was clear that we would need to determine its present distribution and conservation status before being able to develop an effective conservation plan for the species.

The project Antas da Mata Atlântica began in 2005 as part of the IUCN SSC Tapir Specialist Group's mission to determine the distribution and conservation status of each population of the four tapir species. In this study, we focus on *Tapirus terrestris* in the Atlantic Forest biome with the purpose of estimating the size, geographical extent and conservation status of each population. The goal is to provide baseline data to serve as a basis for red listing and conservation actions designed to guarantee the persistence of the species in the biome according to the objectives of the IUCN SSC Tapir Specialist Group.

Methods

Study area

The original size of the biome, today shared by Argentina, Brazil, and Paraguay, spanned 4,000 km of the eastern coast of South America between 3.5°S and 31°S, up to 800 km wide in the south and tens of kilometers wide in the north, with a total forest cover of approximately 1.5 million km^2 (Ribeiro et al. 2009). With annual precipitation between 1000–4000 mm/year and temperatures from <0–40 °C, the biome includes diverse forest types including broadleaf evergreen forest, open broadleaf evergreen forest, broadleaf semi-deciduous forest, deciduous forest, araucaria (*Araucaria angustifolia*) forest, coastal sand soil restinga forests, and mangroves (Gusmão Câmara 2003; Silva and Casteleti 2003). The destruction of the Atlantic Forest is well-documented (Dean 1995; Myers et al. 2000) and recent analysis indicates that only 11.4–16% forest cover remains, most of which is hyper-disturbed and fragmented (Ribeiro et al. 2009).

Third party information

We began working with tapirs in the Atlantic Forest in the 1990s, in Bahia (KF) and São Paulo (EM), and as members of the IUCN SSC Tapir Specialist Group, we maintain regular contact with tapir researchers in the biome. We participated in bi/triennial TSG meetings held during the time of the study, in the Lowland Tapir PHVA Workshop in 2007 and in the ICMBio Red List Assessment for Lowland Tapirs in 2010. At these meetings, 29 scientists working with tapirs in the biome shared their data with us. Topics reported included information about tapir ecology, distribution, and conservation status at the sites familiar to the scientist. During our fieldwork (2005–2020), we received reports from 188 people who provided information on tapir distribution, ecology and/or conservation status, including 161 reserve staff and 25 farmers who had contact with tapirs in the reserve matrix. We grouped the information we received according to categories: background of the person providing the information and details of their contact with tapirs; tapir habitat use and distribution in the forest and matrix lands; threats, including hunting, road-kill,

fires, deforestation, forest degradation; perceived population trends; and conservation actions underway or needed. The details of the reports differed, resulting in variable sample sizes for each information category in the biome-level analysis.

Literature search

Our principal tool was the IUCN SSC Tapir Specialist Group Virtual Library which is a compilation of >800 studies published on the Tapiridae family. We further searched Google Scholar and SciELO using key words and Boolean searches (*Tapirus terrestris*, tapir, anta, Atlantic Forest, Mata Atlântica, names of states, provinces, and reserves). We also searched the web for relevant grey literature, which was mostly master and doctoral dissertations, and searched the bibliography of these documents for other grey literature and publications in regional journals.

Field visits

We searched for tapirs in 93 reserves. Visits mostly lasted 1–3 days per site during which we searched for tapir sign along trails and roads in each reserve, following the advice of reserve staff as to the best locations for finding tapir sign. We collected information on habitat type, levels of human disturbance, condition of the reserve infrastructure, and matrix habitats. For each tapir record, we noted the type of encounter (track, scat, trail, or sighting), habitat type, proximity to water, track size, and GPS location. In cases where tapir tracks meandered along roads, we only considered a tapir as a new individual if there was a distinctive change in track sizes or if we had walked ≥1 km without encountering tapir sign.

Geographic extent and total area occupied

We used the total size of each reserve from the official reserve databases as the area occupied in the cases where reports and/or searches confirmed the presence of tapirs throughout the reserve. In cases where tapirs have expanded their ranges outside of the reserve, we mapped the known use areas, measured the area using Google Earth, and added them to the reserve area. For populations in which tapirs were not distributed throughout the reserve, we delineated the area used on the maps and estimated the area occupied. By summing the respective area occupied by each population, we estimated the total area used in the biome. The use of maps of different scales may have affected the calculation of the area occupied, but we believe this potential error had a negligible effect on the population estimate.

Population estimate

There are few density estimates for Atlantic Forest tapirs; studies use different methods to measure density (Hill et al. 2003; Medici 2010; Bueno et al. 2013; Ferreguetti

et al. 2017), and based on this literature and field visits, it was clear that tapir abundances vary across the biome. Because of this, extrapolating densities from any one estimate is problematic. Instead, we follow Tobler et al. (2013) using a density range of 0.1–0.6 individuals/km^2, densities which fall within the range of most known density data from lowland tapir populations across the species' range, including the Atlantic Forest. To estimate the total biome population, we multiplied the biome area occupied by tapirs by 0.1 and 0.6, respectively.

Population profiles and statistical treatment

We compiled the information gathered into individual population profiles, organized the data by category in Excel spreadsheets, and used descriptive statistics to analyze the biome level data.

Ethical note

We followed all laws regulating research in Brazil. Authorization permit numbers for federal and state reserves were SMA São Paulo 40.624/97, IBAMA 02027.004507/97-84, SISBIO 44897-3, 44897-4, COTEC 232/2016, IAP 65.15, and SEMA 04/2016.

Results

Populations

Our research shows that there are at least 48 populations in the biome (Table 1, Fig. 1), with a population of 2,665-15,992 individuals occupying 26,654 km^2 of the original 1.5 million km^2 of the Atlantic Forest. Tapirs have suffered a 98.2% reduction in its range since European colonization and were extirpated from the Atlantic Forest north of Bahia (the Alagoas population was a reintroduction) and from Rio de Janeiro, but persist in all of the other Brazilian Atlantic Forest states, in Misiones Province in Argentina and in nine forest reserves in eastern Paraguay. São Paulo and Paraná states have the largest number of populations with 14 and 10, respectively, but the two largest populations are those of Misiones and the contiguous Iguaçu and Turvo reserves, in Paraná and Rio Grande do Sul, respectively. The other Brazilian Atlantic Forest states supporting tapirs have 1–4 populations each. Twenty-five populations inhabit the tropics, 22 the sub-tropics, and one spans both. Tapirs inhabit 22 state/provincial reserves, 6 federal reserves, 3 multiple use conservation areas, and a minimum of 29 private reserves. Excluding two outliers (Usina Serra Grande, Alagoas, and Serra da Bodoquena National Park, Mato Grosso do Sul), the mean distance between populations (N=46) is 48 km (SD 35.4). There is no evidence of movement between any of the populations. The tapirs in the Serra da Bodoquena (Mato Grosso do Sul) and Estancias Bello Horizonte/Garay Cue (Paraguay) may be part of larger populations that incorporate the savanna habitats contiguous with the reserves.

Habitat use

Tapirs are adapted to the entire biome, using all of the natural vegetation physiognomies, and tolerating a rainfall spectrum of 1000–4000 mm/year, temperatures from <0 °C to >40 °C, and elevations from 0–1800 m. Third party data and 275 independent tapir records indicate that in 90.2% (N = 41) of the populations tapirs used all of the forest types available. These include primary, logged, secondary, and araucaria forests, pioneer bush, alpine vegetation, grassland enclaves in the forest, sand soil coastal forests, mangroves, and the beach. Tapirs use diverse matrix habitats, including grain fields (oats, wheat, maize, and soy), sugarcane and exotic tree (*Eucalyptus* and *Pinus*) plantations, and smallholder farms. Tapirs from 17 (50%, N = 34) populations raided crops, eating at least 22 cultivars, mostly orchard and commercially produced fruits, but also manioc and bean leaves, rubber trees, wheat, oats, soy, and maize. Reserve staff received complaints from farmers of tapirs causing economic damage to crops in only three cases, and overall tapirs appear to cause negligible losses for farmers.

Matrix permeability and distance moved from the forest edge

Tapirs in 73% (N=37) of the populations leave the reserves to move between fragments, to feed on secondary forest plants in the matrix, to visit reservoir ponds, to rest, and to raid crops. Tapirs that use the matrix often stay near the forest, with 53.6% (N=28) traveling ≤2 km from the edge. Tapirs are capable of long distance movements, however, and in 39.3% of the populations, tapirs travelled up to 3–9 km from the reserve edge, crossing diverse matrix habitats and using small forest patches distant from the main forest block. There were two reports of tapirs moving 20 kilometers south of the Vale Reserve in Espírito Santo, and while these appear to have been rare events, they illustrate the tapir's capacity for long distance travel.

There appear to be few human-made landscape features that create absolute movement barriers for tapirs. Tapirs pass through 4–5 band barbwire fences (100%, N=26) and readily traverse rural and small forest roads (100%, N=32), but highways (≥ 2 lane paved roads) are mostly barriers, with tapirs only crossing them in 20.5% (N=34) of the populations.

Other barriers include chain-link fencing, irrigation canals, walls, and large human settlements, although tapirs do occasionally wander into city neighborhoods (Timóteo, Minas Gerais) and live on the outskirts of several large urban centers (e.g., PESM Núcleo Curucutu and Jurupará State Park, São Paulo; Mata dos Godoy, Londrina, Paraná). With the tapir's capacity for swimming, lakes and rivers should not create movement barriers and reports from the PESM (São Paulo) indicate that they swim under highway bridges to reach forest on the opposite bank.

Table 1. The 48 known Atlantic Forest *Tapirus terrestris* populations in the South American Atlantic Forest.

Population	State	Reserve Category	Size (ha)[c]	Area Tapirs Occupy	Population Estimate[d]	Population Status
1 Usina Serra Grande	AL	P	8,000	<1,000	1–6[e]	?
2 Estação Veracel/Pau Brasil[a,b]	BA	P, F	6,869	6,500	7–39	S
3 Pau Brasil[a,b]	BA	F	25,000+	25,000+	25–150	E
4 Descobrimento[a,b]	BA	F, P	30,000+	30,000+	30–180	S
5 Corrego do Veado[a,b]	ES	F	2,400	2,400	2–14	S
6 Sooretama/Fibria/Vale[a,b]	ES	F, P, P	47,462	47,462	48–285[f]	S
7 Mata Escura[a,b]	MG	F	50,872	? 1,000	1–6	D
8 Limoeira/Vista Bela[a,b]	MG	P	1,000+	1,000+	1–6	S
9 Rio Doce[a,b]	MG	S, P	35,970+	35,970+	36–216	S
10 Caraça[a,b]	MG	P	11,233+	11,233+	11–67	S
11 Serra do Mar (PESM)[a,b]	SP	S	332,000+	~249,000	249–1,494	E
12 Jureia Itatins[a,b]	SP	S	90,000	90,000	90–540	S
13 Jurupará	SP	S	26,251+	26,251+	26–158	S
14 Paranapiacaba[a,b]	SP	S	140,486+	~112,389	112–674	E
15 Serra do Mar SP/PR[a,b]	SP, PR	S, F, P	150,000+	~90,000	90–540	E
16 Guaricana/St. Hilaire-Lange[a]	PR	F, S	74,406+	~44,644	45–268	E
17 Lauraceas[a,b]	PR	S, P	32,000+	~22,400	22–134	E
18 Itapoa	SC	P	1,117+	1,117+	1–7	S
19 Dona Francisca[a]	SC	S	40,178+	~10,000	10–60	?
20 Sassafrás/Corupa[a]	SC	P, S	3,682+	3,682+	4–22	?
21 Serra do Tabuleiro[a]	SC	S, P	84,130+	84,130+	84–505	E
22 Caetetus[a,b]	SP	S	2,178	2,178	2–13	S
23 Rancharia	SP	P	1,500	~1,500	2–9	?
24 Novo Horizonte	SP	P	1,500	~1,500	2–9	?
25 Irapuã	SP	P	1,650	~1,650	2–10	?
26 Valparaiso	SP	P	2,100	~2,100	2–13	?
27 Aguapei	SP	S	9,044	9,044	9–54	?
28 Rio do Peixe	SP	S	7,720	7,720	8–46	?
29 Morro do Diabo[a,b]	SP	S, P	37,000+	37,000+	37–222[g]	E
30 Caiua	PR	S	1,449	1,449	1–9	?
31 Rio Ivinhema/Ilha Grande	PR, MS	S, F, P	149,378	149,378	149–896	?
32 Mosquito[a,b]	SP	P	2,190	2,190	2–13	?
33 Mata dos Godoy[a,b]	PR	S, P	2,600+	2,600+	3–16[h]	E
34 Central Paraná	PR	P	10,000+	~10,000	10–60	?
35 Rio Ivaí	PR	P	≤10,000	~10,000	10–60	?
36 Lageado	PR	P	10,000+	10,000+	10–60	S
37 Araupel	PR	P	14,707	~10,000	10–60	?
38 Misiones/Iguaçu[a,b]	AR, PR	F, S, P	1,000,000	1,000,000	1,000–6,000	S
39 Yaboti/Turvo[a,b]	AR, RS	S, S	316,000	316,000	316–1,896	S
40 San Rafael/Tapyta	PY	F, P	63,226	~25,000	25–150	?
41 Ypeti	PY	P	13,592	13,592	14–82	?
42 Itabo	PY	P	9,885	9,885	10–59	?
43 Limoy	PY	P	14,828	14,828	15–89	?
44 Morombi	PY	P	25,000	25,000	25–150	?
45 Mbaracayu	PY	P	65,000	65,000	65–390[i]	S
46 Ka'i Rague	PY	P	1,859	1,859	2–11	?
47 Bello Horizonte/ Garay Cue	PY	P	5,800	5,800	6–35	?
48 Bodoquena	MS	F	73,000+	~35,000	35–210	?
Total			3,024,262+	~2,665,451	2,665–15,992	

AL – Alagoas, AR – Argentina, Misiones Province, BA – Bahia, ES – Espírito Santo, MG – Minas Gerais, MS – Mato Grosso do Sul, PR – Paraná, PY – Paraguay, RS – Rio Grande do Sul, SC – Santa Catarina, SP – São Paulo. Conservation category: F – Federal Reserve; P – Private Reserve; S – State/Provincial Reserve. Population status: D – Decreasing, E – Expanding, S – Stable,? – No information. [a]Visited by authors; [b]Tapir presence confirmed by authors; [c]+ = Area given is that of the reserve, but the forest extends beyond the reserve boundaries; [d] Numbers rounded, so the summed number does not correspond exactly to the population estimate made by multiplying the total area by 0.1–0.6. [e] Scientist estimate = 12 (Bachand et al. 2009). [f] Scientist estimate = 392 (Ferreguetti et al. 2017). [g] Scientist estimate = 150 (Medici 2010). [h] Scientist estimate = 45 (Góes C, Arasaki M unpublished results). [i] Scientist estimate = 650 (Hill et al. 2003).

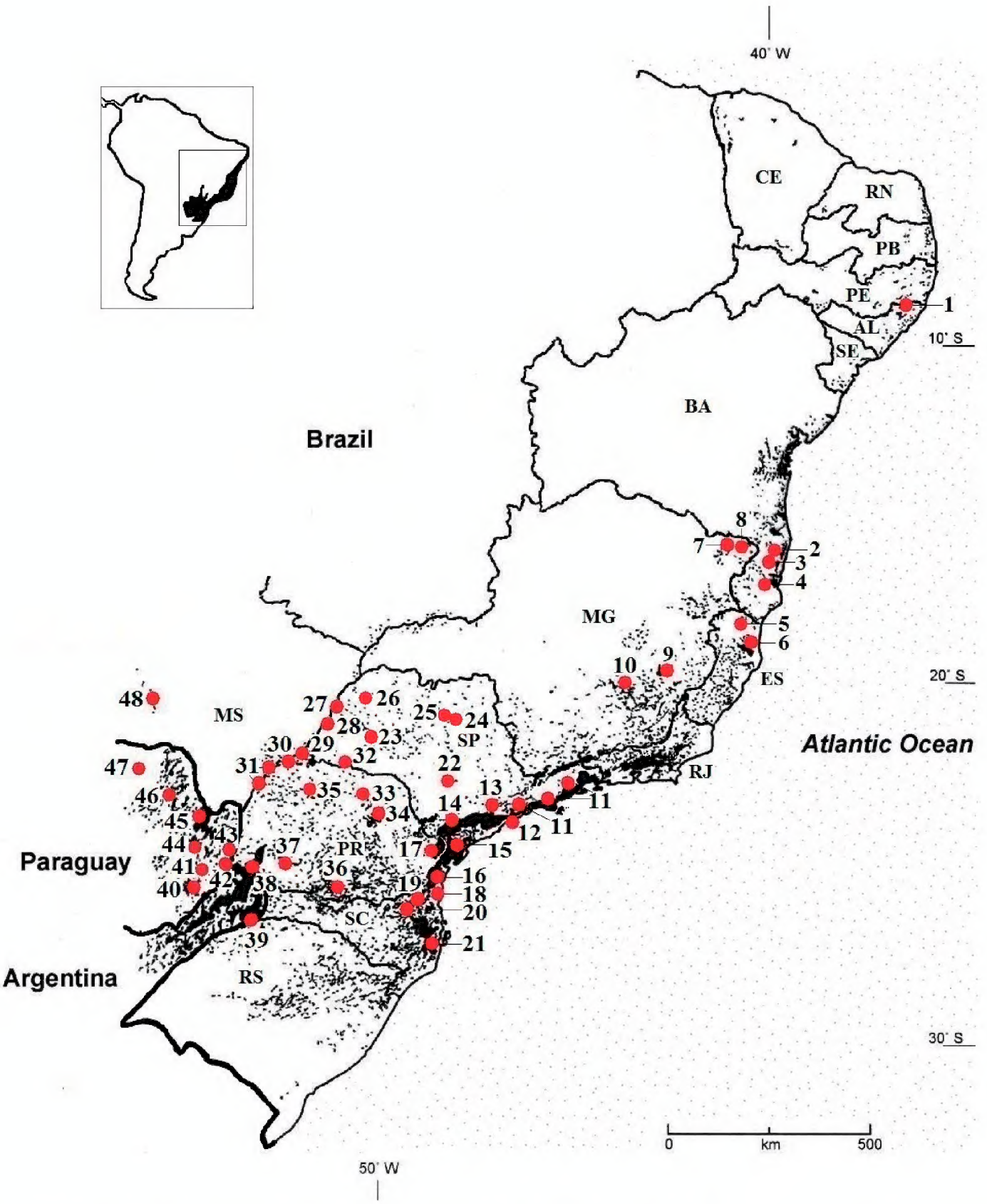

Figure 1. The 48 *Tapirus terrestris* populations in the South American Atlantic Forest. Black speckled area represents the geographical limits and fragmentation pattern of the Atlantic Forest. Each number refers to a particular population with details provided in Table 1.

Conservation status and threats

Reserve staff report tapirs as abundant or common in 62.2% (N=37) of the populations, 15 (60%, N=25) populations appear to have maintained stable numbers over the past decade, and nine (36%) are reportedly growing and expanding their ranges. One population (Mata Escura, Minas Gerais) appears to be at imminent threat of extinction, and one population (Corrego Grande, Espírito Santo) appears to have

been extirpated during the study period. Recent invasions of forest reserves by landless farm workers threaten the Araupel and Lageado (Paraná) populations.

Hunting has historically been the principal cause of tapir declines and extirpations, and in 14 (46.7%; N=30) of the populations there were confirmed tapir kills during the study period. Generalized hunting still occurs in 95.3% (N=43) of the forests inhabited by tapirs. In half of the populations in which tapirs were killed, reserve authorities believed that hunting pressure on tapirs was low, declining or only affecting parts of the reserve, so not an imminent threat to tapir persistence. In the remaining hunted populations, on the other hand, we could not assess the threat of hunting. In some populations, hunting pressure is unevenly distributed, and tapirs are both abundant and scarce/extirpated in the same reserve depending on the locale in question. Commercial hunting was only reported in the PESM (São Paulo) and Veracel (Bahia) populations, retaliation for crop raiding in Yaboti/Turvo (Misiones, Rio Grande do Sul) and Paranapiacaba (São Paulo) populations, with sport/pleasure hunting affecting all of the hunted populations. Subsistence hunting is restricted to Ache people in the Mbaracayu reserve (Paraguay).

Highways present the dual threat of vehicle collisions and movement barriers. Road-kill is a cause of mortality in six of the eight reserves where highways traverse tapir populations, and highway expansion threatens to cause population fragmentation in at least four populations (Sooretama/FIBRIA/Vale, Espírito Santo; PESM, Serra Paranapiacaba/Jurupará, São Paulo; Misiones Green Corridor, Argentina).

Forest loss is ongoing in eleven (25.6%; N=43) forests, but generally on a small scale and is not an imminent threat to tapirs. In some populations (PESM, Paranapiacaba, Jureia-Itatins, São Paulo and Lauráceas, Paraná), forests are actually expanding as former tree plantations, farmlands, and pastures revert to forest both in and outside of reserves.

The history of forest degradation was intense and almost universal, and continues today in the form of generalized hunting, illegal logging, agricultural expansion, fire, and *Euterpe edulis* palm and other plant extraction. Only two populations (Caraça, Minas Gerais, and Kai Rague, Paraguay) inhabit forests with no known ongoing degradation, whereas 22 (51.2%, N=43) populations suffer from two or more forms of habitat degradation. The threat of large-scale logging no longer exists in any of the reserves visited, even though there are still reports of trees being poached on a small scale in nine (21%; N=43) of the forests inhabited by tapirs. Forest fires, normally spreading from neighboring cattle ranches and farms, are considered a serious potential threat to the forest by reserve managers for nine (22%; N=41) of the forests inhabited by tapirs, but we have little information on the impact of these fires on tapirs. However, data from other sites (Medici E personal observation) indicate that tapirs colonize the pioneer vegetation that replaces the mature forest after large fires, so fires do not necessarily make forests uninhabitable in the long-term.

While most populations suffer few direct imminent threats, long-term threats are prevalent, especially those resulting from the isolation of small populations. Gatti et al. (2011) ran Vortex analyses of the minimum number of tapirs required

for long-term persistence in the Atlantic Forest and results indicate that a minimum N_E of 30 and 200 are necessary to ensure demographic and genetic persistence for 100 years, respectively. This means that 33 (68.8%) and 15 (31.3%) of the populations are demographically non-viable, and that 45 (93.8%) and 34 (70.8%) are genetically non-viable, for low and high population estimates, respectively. Only three (6.3%) and 14 (29.2%) of the populations are viable in the long term when considering both variables, for low and high population estimates, respectively. Third party reports indicate that many of the populations have gone through periods with reduced populations that lasted for decades or longer and that the current expansion seen in some populations is from the few individuals that survived near extinction events. These demographic bottlenecks may have already caused the loss of genetic diversity, and the isolation of small populations emerges as the principal threat to tapir persistence in most of the biome.

Law enforcement and conservation financing

Third party reports indicate that 30 (69.8%; N=43) of the tapir populations lack adequate funding for effective protection and monitoring. Of the 15 reserves for which staff report having adequate funding, all but one (Rio Doce, Minas Gerais) were private reserves. The staff of all federal and all state (other than Rio Doce) reserves felt that the lack of adequate financing directly affected their capacity to enforce the laws, maintain infrastructure, and/or adequately monitor wildlife and illegal activities.

Discussion

This study summarizes what we know about the distribution and conservation status of the species at the beginning of the 21st century, and as such, serves as a benchmark for future evaluations of the species conservation status in the biome. The analysis of the 48 populations reveals a variable portrait, with some populations large and expanding and others small and in danger of extinction, presenting a complex mosaic of conservation challenges for securing the persistence of the species in the biome. However, the study revealed several general trends that will help guide the specific conservation actions required for protecting each population.

Population estimate and viability

While all biome level population estimates are problematic when based on scant data, those provided here are likely to fall within the acceptable range of probability (Tobler et al. 2013). Field visits and population estimates from other scientists (Table 1) suggest that most populations tend towards the mid to high end of the population range estimate (0.4–0.6 individuals/km^2), but only further research can confirm this. Furthermore, there remain several lacunas in our distribution data,

the resolution of which will determine exactly how many populations there are. The connectivity of the populations along the principal rivers in the interior of Paraná and São Paulo remains unclear. In the contrasting landscape context of the Paranapiacaba Mountains and Jurupará State Park, São Paulo where the mountains support largely contiguous forests and a matrix of tree plantations, we still do not know whether tapirs are continuously distributed or fragmented. In Misiones, Argentina, the million-hectare forest block, here considered as supporting two isolated populations, may in fact be fragmented into as many as five populations (Pardo et al. 2017). In addition, there are at least nine sites in the biome where there is a small probability of relic tapir populations persisting. Resolving these lacunas should be a priority over the next decade. What is clear even with these remaining lacunas is that few of the populations are either demographically or genetically viable in the long-term, and that overcoming the threat of small population sizes will be the paramount challenge in the coming years.

The causes of isolation

Isolation is the principal long-term threat to tapir persistence in the biome, with up to 93.8% of the populations vulnerable to extinction over the next century due to small population sizes. The Atlantic Forest is severely fragmented with the majority of forests <50 ha and an average distance between fragments of 1440 m (Ribeiro et al. 2009), but this in and of itself should not be a cause of population isolation. Tapirs frequently use matrix lands, traveling up to 9 km beyond the reserve edge, which is greater than the distance between most fragments in the biome. The non-forest vegetation of the matrix also does not appear to be the cause of isolation as tapirs use a wide array of agro/pastoral lands. These non-forest habitats include those generally believed to be hostile to wildlife, such as grain fields, sugarcane, cattle pastures, and eucalyptus and pine plantations (Galetti et al. 2001; Bachand et al. 2009; Medici 2010; Trudel et al. 2010; D'Avila Centoducatte et al. 2011; Begotti et al. 2018). This suggests that forest fragmentation and matrix type are not the cause of isolation per se. In the Mata dos Godoy landscape in Paraná, tapirs regularly traverse grain fields, moving up to 7.5 km between forest fragments, and have persisted in this hyper-fragmented landscape for almost a century (Góes C, Arasaki M unpublished results). The evidence available indicates that agricultural matrix type matters little for tapirs when crossing between forest fragments, and that tapirs will readily cross long distances of non-forest habitat if other factors do not impede their movements.

Forest degradation likewise does not appear to be a factor limiting tapir distributions. *Tapirus terrestris* adapts well to disturbed and secondary forests (García et al. 2012) and we found tapir sign abundant in logged and secondary forests in all stages of succession. It is still unclear whether tapirs can persist in secondary forests without access to primary forests (Ranzani de Luca and Pardini 2017), but the results from our fieldwork suggest that tapirs can thrive in extensive stands of secondary forest, at least several kilometers distant from primary forest groves. In Córrego

do Veado and Sooretama, Espírito Santo and Rio Doce, Minas Gerais where fires burned 30–80% of the reserves (Stallings et al. 1991; Chiarello 1999), tapir sign is abundant in secondary forests decades later. In the upper elevation plateau forests of the Parque Estadual Serra do Mar, São Paulo tapir sign is abundant in extensive tracts of secondary forest regenerating from farms, pastures and exotic tree plantations abandoned 20–50 years ago and where tapirs have no proximate access to primary forest. Dietary studies show that tapirs eat >200 plant species, feeding on bark, twigs, leaves, and fruits (Salas and Fuller 1996; Henry et al. 2000; Bachand et al. 2009; Talamoni and Assis 2009; Tobler et al. 2010; Hibert et al. 2011; Bueno et al. 2013; Ranzani de Luca and Pardini 2017). A wide variety of secondary plants are highly palatable for tapirs (Salas and Fuller 1996; Bachand et al. 2009; Ranzani de Luca and Pardini 2017), and the evidence gathered here and elsewhere (Parry et al. 2007) indicates that the stage of forest succession and the history of disturbance is not a factor limiting tapir distributions.

The principal causes preventing tapirs from crossing matrix habitats to distant forests more effectively appear to be high traffic highways (Medici 2010), hunting (Cruz et al. 2014), dogs (Gatti et al. 2018), chain-link fences and irrigation canals (Chalukian et al. 2009). The highways that traverse the landscapes between extant tapir populations can be sink habitats and/or movement barriers, and where tapirs cross highways, they frequently die in car collisions (Cáceres et al. 2010; Ascensão et al. 2017; Freitas et al. 2017; Poot and Clevenger 2018). The heavily trafficked BR-101 (which traverses the Brazilian Atlantic Forest from the north to south) is a death trap for wildlife, and tapirs periodically die while crossing it between the Sooretama and Fibria/Vale reserves in Espírito Santo (Ferreguetti et al. 2017; Gatti A unpublished results). Road-kill was also a major cause of tapir mortality in Morro do Diabo State Park (Medici E personal observation) and still is in Santa Virginia (PESM) and in the Caetetús reserves in São Paulo. The threat of death while crossing highways may impede tapirs from utilizing/colonizing nearby forests with suitable habitat. In São Paulo, highway BR-101 prevents tapirs from crossing the 1 km forest gap between the PESM and Jureia-Itatins reserves and BR-116 prevents them from crossing between the PESM and Paranapiacaba populations and possibly splits the Rio Turvo population in two. Vehicle traffic in the Atlantic Forest is increasing and there are plans to double the size of many of the major highways, including BR-101. As busy highways lie between each of the extant populations, the threat of roads to tapir persistence and population expansions is likely to increase in the future unless measures are taken to mitigate this. Other barriers to tapir movements, such as chain-link fencing, irrigation canals, electric fences and pipeline infrastructure (e.g., Cubatão in the PESM population, São Paulo), are site specific so the solutions will need to be resolved locally on a case by case basis. The majority of fencing in the biome consists of 4–5 band barbwire fences that tapirs readily cross.

Hunting is the principal historical cause of tapir declines in the biome, and while no longer an imminent threat to most populations, it continues to be the principal reason that tapirs are not more widely distributed in the landscapes surrounding

reserves. Where hunters rarely target tapirs, such as in the Mata dos Godoy, Paraná (Góes C, Arasaki M unpublished results) and Morro do Diabo, São Paulo (Medici 2010), tapirs readily move throughout the landscape, whereas in landscapes where hunters kill tapirs, the species is unable to occupy these areas. In the Lauráceas reserve, Paraná, tapirs are re-colonizing pine plantations to the west where company policies prohibit hunting, whereas in the northern and eastern sections of the reserve in lands adjacent to smallholder farm landscapes, hunters continue to kill tapirs whenever they appear, preventing them from re-colonizing these areas (Mello M unpublished results). The same is true in the PETAR in the Paranapiacaba Mountains, São Paulo where tapirs are abundant in the upper elevation forests and moving out of the reserve where hunting pressure is low, but absent from the lower elevation forests along the Vale do Ribeira where hunting pressure is high. In Misiones, Argentina, tapir abundances increase with distance from hunter access points (Cruz et al. 2014). Intense hunting in the San Rafael reserve in Paraguay limits tapirs to the remote core areas, and may be fragmenting this population from tapirs in the contiguous Tapya reserve (Cartes JL, del Castillo H unpublished results). Dogs are abundant in the countryside in the Atlantic Forest, especially in smallholder landscapes, and in these contexts, dogs (whether accompanied by hunters or not) may prevent tapirs from using the matrix habitats (Lessa et al. 2016). Although third party reports suggest that hunting pressure is falling throughout the biome, it remains a principal reason that tapir populations are fragmented and isolated.

Other potential threats

Deforestation is not an imminent threat to tapir persistence in most of the biome. The rate of forest loss in the Brazilian Atlantic Forest is decreasing (SOS Mata Atlântica/INPE 2018), has been decreasing in Paraguay and not affecting most protected areas (Da Ponte Canova et al. 2016), and has decreased in Misiones (Fundacíon Vida Silvestre Argentina and WWF 2017). There was some forest loss in the greater landscapes of 10 tapir populations, but on a small scale and not in the reserves (with the exception of Araupel, Paraná and San Rafael, Paraguay). Recent studies reveal that afforestation is increasing (Linhares de Rezende et al. 2015; Bicudo da Silva et al. 2017; Costa et al. 2017), and at least on the northwest side of PESM, São Paulo is providing new habitat for tapirs. However, while it is encouraging that the rate of forest loss is decreasing, the small size of most reserves and the continuing threat of landless farmer invasions means that deforestation is still a potential threat to some populations.

Fire is mostly a threat in landscapes where it is used to renovate pastures. Not only can tapirs be killed outright by burning (Trudel et al. 2010), but when fires burn into reserves, the carrying capacity of these reserves decreases in the short-term which could acerbate demographic/genetic threats already existing in small populations. Park staff report that firefighting has improved considerably over the past decade, but fires still do occasionally burn large tracts of forest, so fire is still a threat in reserves that have hard edges with cattle pastures.

The further fragmentation of tapir populations is a threat in the Misiones, Argentina (Pardo et al. 2017) and Serra do Mar populations, especially due to the construction of roads and increasing traffic. This issue is especially relevant because these are the largest populations with the greatest potential for long-term persistence, so finding ways that allow tapirs to traverse highways is an urgent conservation priority.

In addition to causing isolation, hunting is a potential threat to tapir persistence in all of the small populations and affects tapir abundances in large reserves (Hill et al. 2003; Cruz et al. 2014). Vortex simulations clearly show that in small populations, even the loss of a single individual/year can rapidly lead to the extirpation of a population. Even though tapirs are rarely targeted by hunters in the Atlantic Forest (Galetti et al. 2017), individuals are still being lost in small populations either through sport hunting or in retaliation for crop raiding (e.g., Turvo, Rio Grande do Sul). Furthermore, where hunters use rifle traps set for other animals, tapirs can die as a result (Gatti A unpublished results, Córrego do Veado, Espírito Santo). Dogs frequently accompany hunters, but also hunt on their own, and attacked both young and adult tapirs in the PETAR and Intervales (São Paulo), Corrego do Veado (Espírito Santo) (Gatti et al. 2018), and Veracel (Bahia) reserves during the study period. Tobler et al. (2013) show that even low levels of hunting can cause population declines in extensive areas of contiguous forests, so the threat is even more acute in small isolated populations.

Because tapirs are wide-ranging herbivores that may cross human-impacted areas, they are exposed to large-scale agriculture and cattle ranching, contamination by pesticides and heavy metals, and increased exposure to domestic and feral animal diseases. The proximity of lowland tapirs to domestic livestock in several parts of the species distribution creates opportunities for disease transmission (Medici and Desbiez 2012; Medici et al. 2014; Fernandes-Santos et al. 2020).

The inadequate allocation of state and federal funds to conservation is a ubiquitous threat to tapirs because it brings into question the long-term commitment of the governments towards preserving natural areas. Reserve staff throughout the biome complained about inadequate funding and the truth of this complaint was evident when visiting the reserves. Without a fundamental change in support for conservation areas, there is no guarantee for the future of tapirs and other species.

Conclusion

The results of this study give cause for cautious optimism for the future of tapirs in the biome. Tapir conservation status reached its nadir in the 1950–1970s, by which time hunters had reduced tapirs to relic populations tenuously surviving in the most inaccessible forests, and it appeared tapirs were doomed. After decades of dedicated conservation efforts by state and federal officials, non-governmental organizations and scientists, this situation is starting to improve. Deforestation rates in the biome are falling, firefighting efforts are increasingly effective, afforestation is starting to

occur, and the majority of the remaining forests are protected as strict reserves, sustainable use areas, or conservation set-asides. Even though federal and state reserves are grossly underfunded, tapir populations have started to recover, and tapirs are occupying areas where they were absent for decades or longer. Importantly, an increasing number of scientists are studying tapir ecology and the causes of abundances and distributions, information which is essential for developing effective conservation strategies. Today, we know that the biome population is larger than we believed a decade ago; most populations do not suffer overt imminent threats, nine populations appear to be expanding, and we have increasing knowledge of tapir ecology. Successful reintroduction programs provide the experience necessary to allow us to repeat the process throughout the many empty forests in the biome, providing hope that tapirs will continue to re-occupy their ancestral lands.

Challenges remain, however, and addressing the principal threats to tapir persistence will require a long-term effort and a large number of people. The maximum distances recorded for tapir movements outside of the forest are less than the distances between most tapir populations, and population isolation emerges as the principal threat to the species' long-term persistence. Distance is not the only issue, however, and even though tapirs can pass through most barbwire fences, heavily trafficked roads and irrigation canals can be death traps, preventing population expansions and inter-population connectivity even when the distances between populations are small. Hunting, which has historically been a leading cause of the reduced number of tapir, has fallen to the point that it is no longer an imminent threat for the large populations, although still a significant threat in small populations. Diseases transmitted from domestic livestock are a chronic threat as many tapir populations inhabit forests surrounded by pastoral lands, and fires, often spreading from pasture burning, can destroy remaining forests and kill tapirs. Despite these continuing challenges for tapir conservation, most populations appear to be stable or increasing and the conservation outlook for the species is better than it was when the first efforts to protect the species began several decades ago. The evidence provided here suggests that tapirs could be much more widely distributed in the biome, and that with appropriate conservation actions, tapirs should be able to inhabit many of the human-dominated landscapes typical of the Atlantic Forest.

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